FORAGING BEHAVIOUR OF THE BROWN TREE SNAKE, *BOIGA IRREGULARIS*

GORDON H. RODDA

Arizona Cooperative Fish and Wildlife Research Unit, 210 Biological Sciences East, University of Arizona, Tucson, AZ 85721, USA

ABSTRACT

Boiga irregularis is a nocturnal, primarily arboreal, rear-fanged colubrid that is believed to have eliminated most of the native forest vertebrates on the island of Guam. On Guam it usually eats birds, rats, and lizards, including both day and night active species. To determine where the snakes forage, I tabulated 398 sightings of foraging snakes, recording their perch height, perch diameter, and perch plant species. These measures were compared to the places where searchers look for snakes, as well as the heights and perches where likely prey items are seen. Snakes were seen less often than would be expected based on search effort at heights from 2-5 m above ground. The modal height for foraging snakes was less than 0.5 m and they exhibited no preference for perch diameter. To determine how the snake locates its prey I watched 26 snakes for a total of 19.45 hours using a night-vision device. Both active search and ambush foraging modes were evident, with many snakes using both tactics within an evening. The postures adopted by immobile snakes suggest that they could detect the odor tracks of geckos. I also observed one medium-sized snake consume a sleeping adult columbid bird, which it found by active search.

INTRODUCTION

The brown tree snake, *Boiga irregularis*, has been associated with the loss of most native birds, bats, and lizards on the island of Guam (Savidge, 1987; Wiles, 1987; Fritts, 1988; Engbring & Fritts 1988). In addition, it has been held responsible for hundreds of power short-circuits (Fritts, Scott & Savidge, 1987), loss of agricultural and pet animals (Fritts & McCoid, 1991), and envenomation of human babies (Fritts, Scott & Smith, 1989; Fritts, McCoid & Haddock, 1990). Shortly after World War II the brown tree snake was accidentally introduced to Guam, an island lacking snakes as predators on vertebrates. By the 1980s the snake had reached localized population densities in excess of 50/ha (Fritts, 1988; Rodda, Fritts & Conry, 1992). Ongoing efforts to reverse or minimize the adverse impacts of the introduction have been hampered by lack of understanding of the behaviour of the snake.

Although the snake's predation on native vertebrates has attracted considerable attention, information on how the snake obtains these items has been limited to what may be inferred from stomach contents (Savidge, 1988; Greene, 1989; Shine, 1991). The snake had not been observed capturing prey in the wild. The gut samples indicate that the brown tree snake has a remarkably catholic diet, including all life stages (eggs, juveniles, adults) and all species of small terrestrial vertebrates. Its length (up to 3.0 m) also allows the consumption of smaller representatives of the larger vertebrate species. For example, on Guam the snake is well known for its attacks and feeding attempts on German shepherd puppies (Fritts, 1988). In general, smaller brown tree snakes consume mostly lizards while larger individuals eat primarily endotherms (Greene, 1989).

Both diurnal and nocturnal species are preyed upon; the snake is nocturnal (Fritts *et al*. 1987). These observations imply that both active and inactive prey items are taken. Likewise, the consumption of immobile bird and lizard eggs would seem to require an active foraging mode, whereas nocturnal rats and geckos might be most easily captured by ambushing. Although most snakes are thought to specialize in a particular foraging mode, the breadth of this snake's dietary proclivities suggested that it would exhibit both ambushing and active foraging modes.

The length of time that a foraging snake remains at a site ("giving up time") reflects its dependence on the ambushing

tactic. Determining the "giving up time" of a foraging animal is also useful for testing the applicability of optimal foraging models (e.g. Schoener, 1971). In *Lachesis muta*, an ambushing pit viper, the "giving up time" is about two weeks (Greene & Santana, 1983). In contrast, actively foraging snakes such as *Nerodia* may move more or less continuously when foraging (Mushinsky & Hebrard, 1977). One objective of this study was to quantify the "giving-up time" of foraging brown tree snakes.

To design measures for control or eradication of the brown tree snake it is vital to know exactly where and how foraging takes place. Traps or capture programs directed at ground level may be futile if the snakes are foraging primarily in the forest canopy. Traps set on tree trunks might not work if foraging occurs primarily in foliage. In this paper I report on the distribution of snake sightings with reference to perch height, perch diameter, and perch plant species, both in absolute terms and in relation to the typical positions occupied by geckos, the snake's primary nocturnal lizard prey. In addition I report the moves and postures of foraging brown tree snakes, as observed with the aid of a night-vision device.

METHODS

As a consequence of recurrent typhoons and other habitat disturbances, most of the forests on Guam are short in stature (< 10 m). Therefore, brown tree snakes can be found by visually scanning trees at night. The snake sightings reported below were made at four forested sites on Guam: Orote Point plateau, Naval Communications Area Master Station overlooking Haputo Beach, along the road to Ritidian Point, and in the forest west of Northwest Field. In 398 observations of snakes made by myself or Renée Rondeau in Feb.-Oct. 1988, we estimated each snake's height above ground, perch diameter and the perch plant species. During the same censuses we also estimated the value of these parameters for all geckos seen (n = 890) and for the places that we were searching for snakes (n = 1611 spot samples). The spot samples consisted of our records of the plant species and perch heights that we were viewing, at the instant an unpredictable alarm sounded. A conscious effort was made to scan all vegetation and to scan it at a constant rate. While these data are only estimates, they give an indication of where most snakes were seen and whether these places also contained visible geckos. I quantified the positions of geckos not only because they are preyed upon by the snake, but also because the

observability of small geckos is less than that of brown tree snakes to a human searcher. All the geckos were relatively small; more than 95% were *Lepidodactylus lugubris* and *Hemidactylus frenatus*. A typical snout-vent length for a *Lepidodactylus* was 35 mm, that for *Hemidactylus* 45 mm, and that for *Boiga* 950 mm. Thus the decline in number of snake sightings at greater distances from the observer can be compared to that in more cryptic reptiles.

Using a night-vision device I watched 26 foraging snakes at various times between 14 February 1988 and 19 June 1989, for a total of 19.45 h. I used both monocular (Litton Industries M-845) and binocular (Litton Industries M-802A) devices, providing both magnification and photo-amplification. In some cases the naturally available light was augmented by light from adjacent street lamps; as the snakes had entered these dimly lit areas of their own volition, I assume that their behaviour was normal for these conditions. In the absence of moonlight, snakes were extremely difficult to detect with the devices in natural forest or on the ground. Lack of detectability was particularly a problem when the vine-like snakes stopped moving for long periods of time (e.g. hours). Under these circumstances I sometimes augmented the natural illumination with a stationary unfocused headlamp directed into the ground at an angle of at least 60° from the snake. This procedure did not greatly increase the ambient light level; the only light that reached the snake was that which was reflected off the dull soil or herbs, but it was enough additional light that the snake could be unequivocally detected with the photo-amplifying device (though not with the unaided eye).

During 1.33 h of observations I looked for evidence that the snakes' movements were disrupted by light. Snakes that had been directly illuminated by a moving light (i.e. not a fixed streetlamp) generally stopped moving while the light was on them and rapidly moved away from the light source after the illumination had passed. Snakes that were closely approached (approx. 2 m) with a light sometimes moved rapidly away. Therefore, only observations made without directly or closely illuminating the snake are included in the following results. With one exception (see below), the minimum viewing distance was approximately 7 m; a typical viewing distance was about 15 m.

Most of the observations (15 snakes; 14.08 h) were made on a chain link fence bordering the Naval Air Station-Agana. This site was chosen for the large number of snakes present and the relatively good visibility of snakes on the fence. The natural behaviour of these fence-climbing snakes is corroborated by a smaller number of observations (11 snakes; 4.04 h) made of snakes in the forest.

Foraging mode and predatory tactics may vary from site to site depending on prey availability. At the fence site, the most likely prey was geckos, both because the snakes were predominantly of a size that would eat geckos, and because geckos were extremely abundant on the fence. All types of prey were less abundant in the forest, and the average snake was larger in the forested areas (Rodda *et al.*, 1992). In the forest site, geckos may have been less important as a prey item than rats.
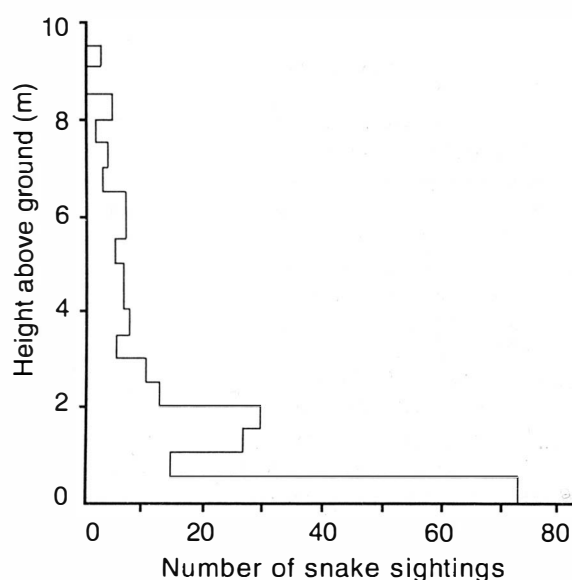

Fig. 1. Distribution of brown tree snake sightings by height above ground.

Height(m)	Compared to places viewed			Compared to lizards seen		
	Snakes	Viewed	Deviation	Snakes	Lizard	Deviation
0-1	41.4	37.2	4.1	13.6	15.9	-2.4
1-2	26.1	24.6	1.4	37.9	36.6	1.2
2-3	9.9	16.0	-6.1	14.3	19.3	-5.0
3-4	4.9	9.5	-4.6	8.6	12.0	-3.5
4-5	4.9	6.3	-1.4	7.1	9.1	-2.0
5-6	4.9	3.0	1.9	7.1	4.4	2.8
6-7	3.9	2.4	1.5	5.7	1.4	4.3
>7	3.9	0.8	1.3	5.7	1.1	2.1
	$G_{adj} = 24.47, P = 0.0009$			$G_{adj} = 23.20, P = 0.0016$		

TABLE 1. Independence of height distributions between snake sightings and either visual searching effort or lizard sightings. For ease of interpretation the values in the body of the table are percent of sample; statistical results were based on the raw frequencies.

RESULTS

HEIGHT ABOVE GROUND

Although the brown tree snake readily ascends to great heights, we saw 77% of the snakes within 3 m of the ground (Fig. 1). Snakes that were foraging high in the trees were slightly more difficult to see than those closer to eye level, but the distribution of sightings (Fig. 1) is not entirely due to the greater difficulty of seeing snakes at greater distances. For example, consider two layers of the forest matched for distance from the observer's eyes, one 1-2 m above the eyes, the other an equal distance below: 41% of the total sample was seen in the lower level, whereas less than 5% was seen in the higher layer. This difference was not due to the snakes being easier to spot when they are viewed from above: the shiny yellow/white venter of a brown tree snake is more easily spotted than is the dull brown dorsum. However, the number of snakes seen at low heights may not be attributable to a preference of snakes for low heights: in the places searched (mostly roadsides) there is more vegetation at low heights. The distribution of plant heights along roadsides was not measured directly, but 78% of our searching time was devoted to plant surfaces below 3 m in height. Compared to the places viewed, more snakes were seen near the ground, and fewer snakes than expected were seen at heights from 2-5 m (Table 1). Compared to the heights where geckos were seen, the snakes were seen less often than expected within 1 m of the ground and at heights from 2-5 m. A higher proportion of the snakes than that of the lizards was seen at heights above 5 m (Table 1).

PERCH DIAMETER

Brown tree snakes, even large ones, often crawl through the foliage, being supported by many small twigs. All sizes of snakes also readily crawl along stout limbs. This diversity of pathways is reflected in the absence of any correlation between perch diameter and snake length ($r = -0.03$, $P = 0.7$; Fig. 2). The perch diameters in Fig. 2 have been log transformed to obtain a normal distribution. Data from ground foraging snakes have been eliminated from this figure and the above correlation.

PLANT SPECIES

Table 2 shows significant independence between plant species viewed and plant species occupied by snakes. The distribution of plant species was marginally insignificant ($P = 0.08$) for the snake - lizard contrast. Compared to the places viewed, snakes were more likely to be seen on herbs and *Leucaena*, and less likely to be seen on "other trees". Most (93%) of the sightings in the herb category were on partially bare soil or close cropped grass, where visibility of snakes is exceptionally good. *Leucaena leucocephala* is a legume that folds its leaflets at night, which enhances snake visibility. In contrast to *Leucaena, Casuarina,* and *Scaevola,* the "other trees" had relatively dense foliage and therefore poor visibility for snake sightings.
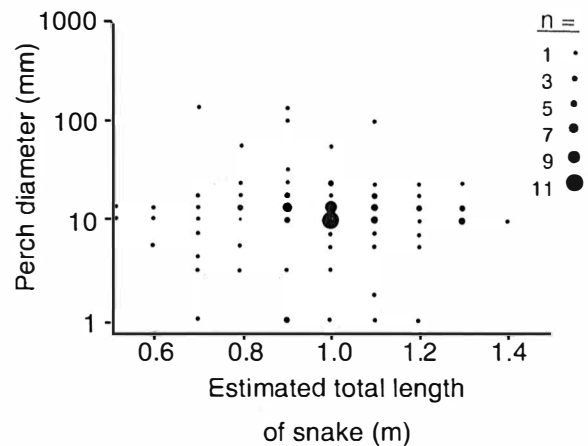

Fig. 2. Perch diameter in relation to snake size. Area of point represents frequency of sightings, as indicated.

Plant type	Compared to places viewed			Compared to lizards seen		
	Snakes	Viewed	Deviation	Snakes	Lizard	Deviation
HERBS	32.7	23.8	8.9	1.4	2.5	-1.1
VINES	3.9	4.0	-0.2	5.7	1.6	4.0
CASUARINA	2.0	2.2	-0.3	2.9	2.6	0.2
SCAEVOLA	6.3	4.5	1.8	9.3	5.6	3.6
LEUCAENA	47.8	43.3	4.5	70.0	75.4	-5.5
OTHER TREES	7.3	21.9	-14.6	10.7	11.9	-1.3
	$G_{adj} = 31.32$, $P = 0.000$			$G_{adj} = 9.72$, $P = 0.084$		

TABLE 2. Independence of plant species distributions between snake sightings and either visual searching effort or lizard sightings. Observations tabulated by major tree species and other plant habit types. Values are percentages of sample, analysed as in Table 1.

DIRECT OBSERVATIONS OF FORAGING BEHAVIOUR

Of the 26 snakes watched, four were discovered on the ground. Three of these were detected on nights with bright moonlight; these vanished in less than 15 seconds. The other was observed for 0.22 h without moonlight. This snake was the exception to the 7 m minimum viewing distance, as it could not be seen without closely approaching it. After a few minutes it appeared to detect the observer and fled rapidly. The 22 remaining snakes were all above ground when first detected. They were watched for periods ranging from 0.07 h to 2.62 h (mean = 0.87 h, S.D. = 0.68 h). Twelve snakes adopted a distinct ambushing posture at some time during the observations. This posture consisted of a motionless body more or less stretched out horizontally, with a distinct S curve in the neck region and the head held motionless very near (< 2 cm) a tree trunk or upright post. For ten of the twelve snakes seen in this posture, the snake either held this posture at the time it was first seen, or the snake maintained this posture until it was disturbed or observations were otherwise discontinued. Thus most of the recorded giving up times are minima. The twelve measured giving up times averaged 32 min (S.D. = 27 min), with the two uninterrupted ones being 10 min and 31 min in length. However, as shorter times would be more likely to be seen from start to finish, these complete intervals may not be representative. One snake was observed motionless in an ambush posture for 1 h 32 min before observations were discontinued.

Of the 22 snakes seen above ground, 16 crawled at some time during the observations. Crawling was usually accompanied by slow exploratory motions of the head, often with reversals of the prevailing movement direction. The net travel rate of the actively foraging snakes was low, and varied from 0 to 26 m/h (mean = 11.4 m/h, S.D. = 7.9). On only four occasions did I witness an undisturbed snake moving rapidly. In one case a snake climbed a fence very rapidly as a house cat approached. This was the only observed interaction with a non-human predator; the cat did not appear to detect the snake. On two occasions snakes bolted at the start of heavy rainfall. No obvious cause was associated with the fourth example of rapid movement.

One snake was observed to catch a prey item during observations. This snake was climbing the cross beam of a high voltage power line (inoperative at the time), when it seized a sleeping pigeon or dove by the head. The snake was about 1.2 m total length; thus the prey was relatively large for this snake. On the horizontal surfaces on which captive snakes are fed, brown tree snakes usually constrict prey that are large and struggling (personal observation; Chiszar, personal communication), but in this case the struggling bird fell off the beam and the snake appeared incapable of pulling it back up (the snake's tail was coiled around the beam as an anchor). After 22 min of the snake hanging off the beam with the bird in its mouth, the snake pulled the apparently dead bird back up to the beam and began swallowing it. Swallowing took 120 min, after which the grotesquely bulging snake began slow exploratory movements and I discontinued the observations.

DISCUSSION

FORAGING HEIGHT

Although the brown tree snake has a morphology and locomotor skills associated with advanced arboreality (Chiszar, 1989), on Guam the snake appears to spend much of its time foraging on or near the ground (Fig. 1). This foraging behaviour probably reflects a relatively greater amount of foliage near the ground in the shrubby second growth areas characteristic of Guam. It may also reflect a dietary shift towards preying on skinks sleeping on the ground instead of the nocturnal arboreal geckos (which have been depleted in many areas of Guam: Rodda & Fritts, 1992). Savidge (1988) found that the most common item in brown tree snake stomachs from Guam was skinks.

The relatively large amount of foraging near the ground implies that measures to control the snake could be effective even if limited to heights easily reached by humans. Many snakes can be caught or trapped from ground level. However, substantial amounts of snake activity occurs at all levels in the forest (Fig. 1), and it is possible that individual snakes restrict their foraging to the canopy; thus total eradication may not be possible using exclusively ground level measures.

PERCH DIAMETER

Unlike certain *Anolis* lizards (Scott, Wilson, Jones, & Andrews, 1976), brown tree snakes use all perch sizes (Fig. 2). For so large a snake the modal branch diameter was relatively thin (10-20 mm). The large number of slender branches in a forest and the diverse paths taken by the snakes suggest that brown tree snakes will not be concentrated along any particular pathway. Traps and other control measures may need to be placed in a wide variety of positions.

PLANT SPECIES

I interpret the distribution of plant species to reflect primarily the visibility of snakes (Table 2). *Leucaena*, for example, may have a greater proportion of snakes, or the snakes that are on *Leucaena* may simply be more visible. Without additional information indicating a concentration in certain plant species, it may be best to distribute traps and other control measures on a wide variety of plant species.

FORAGING MODE

Brown tree snakes exhibit both ambush and active foraging modes on a regular basis. Most snakes appeared to use both modes on a single night. Brown tree snakes may maintain an ambushing posture for several hours, but most also moved during a night. The active foraging mode facilitates the applicability of control measures, whereas ambushing snakes would have relatively few opportunities to encounter a trap or other control device. It may be advisable to bait traps with prey stimuli that are appropriate to active foraging modes (e.g. bird odors), as opposed to stimuli appropriate to ambush mode (e.g. geckos). However, Rodda, Rondeau, Fritts & Maughan (1992) found that gecko baited traps were more successful than similar traps baited with bird odors. Perhaps the bird odors used were a weaker prey stimulus than a live gecko. Much more information is needed on the attraction stimuli needed to maximally entice foraging snakes to enter traps. For example, the foraging snakes appeared to choose the sites at which to adopt an ambushing posture. Do they identify these sites based on the odor trails left by the passage of geckos or other food items? Fritts (pers. comm.) found that brown tree snakes could detect the prior passage of another brown tree snake, presumably by olfactory means. Thus it seems plausible that brown tree snakes could also detect the prior passage of prey items, as Chiszar, Melcer, Lee, Radcliffe & Duvall (1990) has shown for *Crotalus viridis*.

In summary, the brown tree snake appears to be a very adaptable forager, capable of taking a wide variety of prey from a wide variety of places using a variety of foraging tactics. The snake's success as an invader on Guam may in part be due to this adaptability. To the wildlife manager, this variability offers diverse opportunities for attracting and contacting this pest species. The drawback to the brown tree snake's adaptability is that efforts to exclude the snake will necessitate blocking a multitude of pathways.

ACKNOWLEDGEMENTS

REFERENCES

Chiszar, D. (1989). Behavior of the brown tree snake, *Boiga irregularis*: A study in applied comparative psychology. In *Contemporary issues in comparative psychology*, 101-123. Dewsbury, D. (Ed). Sunderland, MA: Sinauer Assoc., Inc.

Chiszar, D., Melcer, T., Lee, R., Radcliffe, C. W. & Duvall, D. (1990). Chemical cues used by Prairie Rattlesnakes (*Crotalus viridis*) to follow trails of rodent prey. *J. Chem. Ecol.* **16**, 79-86.

Engbring, J. & Fritts, T. H. (1988). Demise of an insular avifauna: the brown tree snake on Guam. *Trans. Western Sect. Wildl. Soc.* **24**, 31-37.

Fritts, T. H. (1988). *The brown tree snake, Boiga irregularis, a threat to Pacific islands.* Washington, DC: US Fish Wildl. Serv., Biol. Rep. **88**(31).

Fritts, T. H. & McCoid, M. J. (1991). Predation by the brown tree snake on poultry and other domesticated animals in Guam. *The Snake* **23**, 75-80.

Fritts, T. H., McCoid, M. J., & Haddock, R. L. (1990). Risks to infants on Guam from bites of the brown tree snake (*Boiga irregularis*). *Amer. J. Tropical Med. Hygiene* **42**, 607-611.

Fritts, T. H., Scott, N. J., Jr. & Savidge, J. A. (1987). Activity of the arboreal brown tree snake (*Boiga irregularis*) on Guam as determined by electrical power outages. *The Snake* **19**, 51-58.

Fritts, T. H., Scott, N. J., Jr. & Smith, B. E. (1989). Trapping *Boiga irregularis* on Guam using bird odors. *J. Herpet.* **23**, 189-192.

Greene, H. W. (1989). Ecological, evolutionary, and conservation implications of feeding biology in Old World Cat snakes, genus *Boiga* (Colubridae). *Proc. Calif. Acad. Sci.* **46**, 193-207.

Greene, H. W. & Santana, M. A. (1983). Field studies of hunting behavior by bushmasters. *Amer. Zool.* **23**, 897.

Mushinsky, H. R. & Hebrard, J. J. (1977). Food partitioning by five species of water snakes in Louisiana. *Herpetologica* **33**, 162-166.

Rodda, G. H., Fritts, T. H., & Conry, P. J. (1992). Origin and population growth of the brown tree snake, *Boiga irregularis*, on Guam. *Pac. Sci* **46**, 46–57

Rodda, G. H., & Fritts, T. H. (1992). The impact of the introduction of the brown tree snake, *Boiga irregularis*, on Guam's lizards. *J. Herpetol.* **26**, 166–174

Rodda, G. H., Rondeau, R. J., Fritts, T. H., & Maughan, O. E. (1992). Trapping the arboreal snake, *Boiga irregularis. Amphibia-Reptilia* **13**, 47–56.

Savidge, J. A. (1987). Extinction of an island forest avifauna by an introduced snake. *Ecology* **68**, 660-668.

Savidge, J. A. (1988). Food habits of *Boiga irregularis*, an introduced predator on Guam. *J. Herpet.* **22**, 275-282.

Schoener, T. W. (1971). Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* **11**, 369-404.

Scott, N. J., Jr., Wilson, D. E., Jones, C., & Andrews, R. M. (1976). The choice of perch dimensions by lizards of the genus *Anolis. J. Herpet.* **10**, 75-84.

Shine, R. (1991). Strangers in a strange land: ecology of Australian colubrid snakes. *Copeia* **1991**, 120–131.

Wiles, G. J. (1987). Current research and future management of Marianas Fruit Bats (Chiroptera: Pteropodidae) on Guam. *Australian Mammalogy* **10**, 93-95.